The Contribution of Ant-Plant Protection Studies to Our Understanding of Mutualism

Judith L. Bronstein

Stable URL:

http://links.jstor.org/sici?sici=0006-3606%28199806%2930%3A2%3C150%3ATCOAPS%3E2.0.CO%3B2-Q

Biotropica is currently published by The Association for Tropical Biology and Conservation.

The Contribution of Ant-Plant Protection Studies to Our Understanding of Mutualism[1]

Judith L. Bronstein

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

ABSTRACT

One common class of ant-plant mutualism involves ants that defend plants from natural enemies in return for food and sometimes shelter. Studies of these interactions have played a major role in shaping our broad understanding of mutualism. Their central contribution has come via their development of approaches to measuring the benefits, costs, and net outcomes of mutualism, and their explicit consideration of variability in all of these phenomena. Current research on these interactions is suggesting ecological and evolutionary hypotheses that may be applicable to many other forms of mutualism. It is also generating comparative data for testing the few general theories about mutualism that currently exist.

Key words: ants; extrafloral nectaries; herbivory; mutualism; myrmecophytism; protection; reward.

MUTUALISMS ARE UBIQUITOUS AND IMPORTANT INTER-ACTIONS in natural communities, particularly in tropical environments. Contrary to a widespread belief that biologists have largely neglected these interactions, a great deal of information is now available about many mutualisms, particularly those in which plants and animals interact (Bronstein 1994a). For example, there is an extensive literature documenting the animals that visit plants and the subset of those animals that confer some kind of beneficial service. The specifics of many of these services (such as pollination and seed dispersal), as well as the rewards that plants produce in order to attract them (such as nectar and fruit), are also relatively well known. On the other hand, surprisingly few broad conclusions can yet be drawn that cut across the boundaries of mutualisms conferring different types of benefits. Numerous obstacles have slowed the development of the kind of synthetic view of mutualism that has long existed for other interactions, particularly competition and predation. These include a paucity of widely-recognized general questions about mutualism and a lack of standardized, robust methodologies with which to investigate the few that do exist (Bronstein 1994a).

Ant-plant interactions have made a striking contribution to our nascent understanding of mutualism. In part, this surely reflects the extraordinary ubiquity of ants. However, ants also seem particularly prone to evolving mutualisms with plants.

This tendency has been argued to be an outcome of traits such as their nutritional requirements, aggressive behaviors, and colony organization (Beattie 1985, Davidson & Epstein 1989, Davidson 1997). The abundance of ant-plant mutualisms is particularly notable in tropical habitats. Davidson (1997) argues that the ant species dominating many rain forest canopy samples are subsidized on either plant or insect exudates. Schupp and Feener (1991) show that one-third of the woody plants on Barro Colorado Island (Panama) offers ant rewards and hence are likely to be ant defended. Fonseca and Ganade (1996) have documented a density of 377 myrmecophytic plants/ha in a Brazilian rain forest, while Rico-Gray (1993) has discovered 312 ant-plant associations at one coastal site in Mexico.

Ants confer three primary kinds of services to plants: protection from natural enemies, seed dispersal, and occasionally, pollination (Beattie 1985). The focus of this paper is on ant-plant protective mutualisms, both those involving specialized plant-inhabiting ants (myrmecophytism) and looser relationships in which ants live away from plants but visit them for food. Ants' roles as seed dispersers and pollinators are certainly ecologically and evolutionarily important (e.g., Davidson & Morton 1981, Beattie 1985, Hanzawa et al. 1988, Peakall & Beattie 1991, Gómez & Zamora 1992, Hughes & Westoby 1992, Levey & Byrne 1993). They are particularly interesting for what they reveal about the ecology of pollination and seed dispersal, which are in fact by far the most-studied mutualisms (Fig. 1). However, they arguably have not contributed disproportionately to our *general* understanding of
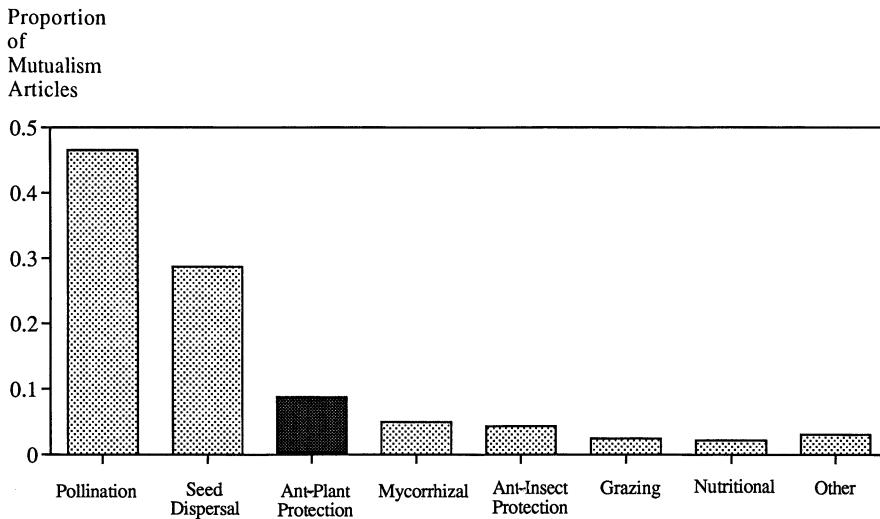
Proportion
of
Mutualism
Articles

FIGURE 1. Frequency of articles on different forms of mutualism published from 1986 to 1995. Of 12,699 articles published during this period in *Ecology, Ecological Monographs, Biotropica, American Naturalist, Evolution, American Midland Naturalist, Journal of Ecology, Journal of Animal Ecology, Oikos,* and *Oecologia,* 4146 (32.6%) were on some form of interaction and 675 (5.3%) on some form of mutualism. More than one form of mutualism was examined in 2.4 percent of the mutualism articles (Bronstein 1994a, pers. obs.)

mutualism in the same way as ant-plant protective mutualisms. Protective mutualisms have been far more commonly studied in the context of questions about mutualism than have pollination and seed dispersal; in these latter cases, the usual focus is on the life history of one of the two partners (Bronstein 1991, 1994a). Ant-plant protective interactions consequently figure prominently as important examples of most of the few broad generalizations that have been drawn about mutualism, even though they are a distant third in terms of frequency of study by ecologists (Fig. 1). Moreover, they provided the first examples of several of these important generalizations.

In this essay, I identify three major directions in mutualism studies in which research on ant-plant protective interactions has played a central role. I will also point out places where these studies can provide a model for research on other mutualisms.

DEMONSTRATION OF MUTUALISM

Mutualism can be defined as an interspecific interaction involving net mutual benefits: members of two species experience higher fitness when they occur together than when they occur alone. Despite their clearly reciprocal nature, most recent studies

of mutualism (95%; Bronstein 1994a) attempt to measure benefits for only one of the two partner species. This is a major problem, since it raises the possibility that interactions will be misclassified as mutualistic when in fact they are commensal or antagonistic, and vice versa (Beattie 1991, Cushman & Beattie 1991). However, measuring benefits for one partner does represent a major advance, since at one time it was rare to quantify benefits for *either* partner. In place of rigorous documentation, biologists argued for mutualism based either on the existence of apparent adaptations to attract or reward partners, or on assumptions about the services those partners should be able to provide. Many long-standing controversies about mutualism have revolved around the question of whether certain interactions do in fact confer benefits. For example, it has been debated extensively whether or not herbivory can ever benefit plants (Owen 1980, Belsky 1986, Paige & Whitham 1987, Bergelson & Crawley 1992). Such debates have been resolved (or, at least, the critical variables have been identified) by quantitative studies that documented the magnitude of benefit, often under a range of densities and ecological conditions. As a rule, these studies employed experiments in which the success of one partner was compared in the presence and absence of its putative mutualist (*e.g.,* for grazing interactions see Allward & Joern 1993).

Some of the first interspecific interactions to gain widespread attention from evolutionists, and the first in which debates about apparent mutualisms were resolved with the use of exclusion experiments, involved plant-associated ants. Extrafloral nectaries had long been noted to attract ants, but whether or not they had any adaptive significance was extensively debated; "protectionists" argued that extrafloral nectaries functioned to attract herbivore-attacking ants, while "exploitationists" held that nectaries merely secreted waste products and their visitors were strictly benign (Beattie 1985). The first ant-exclusion experiment, conducted in 1889, demonstrated that nectary-visiting ants did in fact reduce levels of plant damage (von Wettstein 1889 *in* Beattie 1985). However, since few researchers ever actually observed ants attacking herbivores, doubts persisted about their adaptive function until further exclusion experiments were conducted in the late 1970s (*e.g.,* Bentley 1977a, O'Dowd 1979).

These later studies were stimulated in part by the resolution of another dispute regarding the benefit of ants, this one involving species having more intimate associations with plants. A protective function for ants that occupy living tissue of certain tropical plants had been postulated by Belt (1874) and other early naturalists. Later researchers, including well-known myrmecologists such as William Wheeler, strongly disputed that these ants were beneficial to plants, but never tested this hypothesis directly (Beattie 1985, McKey 1988). Ant-plant interactions then fell into neglect for a half-century. Interest revived dramatically when Janzen published the results of a pathbreaking series of studies on ant-acacias (Janzen 1966, 1967a, b, 1973, 1975). Via ant-exclusion experiments, Janzen (1966) directly demonstrated the degree to which ants can protect plants from herbivory and encroaching vegetation; deprived of their mutualists, ant-acacias could not survive in the field.

The fact that 44 percent of ant-plant protection studies and 57 percent of all mutualism studies published in the last ten years are experimental in nature (Bronstein 1994a, pers. obs.) probably attests to the impact of Janzen's study. Over half of these recent experiments on ant-plant systems basically replicate Janzen's approach: they quantify the consequences of ant exclusion, whether on rates of herbivory (*e.g.,* Vasconcelos 1991), plant growth rates (Schupp 1986, Mahdi & Whittaker 1993), or plant reproductive success (Barton 1986). Similar exclusion experiments have become central in studies of other mutualisms as well. For instance, recent experiments have documented the benefits that mycorrhizae confer on their host plants by killing or preventing colonization of the fungal partner, then examining host performance in the absence of the fungus (*e.g.,* Hartnett *et al.* 1994, Newsham *et al.* 1994).

Note that every example I have given in which benefits were measured in ant-plant protection studies involves calculations of how ants benefit plants. How large, however, is the benefit to the ants? Is that benefit sometimes so negligible that it would be inappropriate to consider the interaction to be a mutualism? These troubling questions remain largely unaddressed by researchers (Beattie 1991; but see Cushman *et al.* 1994 for an attempt to measure benefits to ants in an ant-lepidopteran protective mutualism).

VARIATION IN THE BENEFITS OF MUTUALISM

Most exclusion experiments have shown that ants can in fact benefit plants, usually by reducing the impact of herbivory. The magnitude of that benefit, however, varies greatly. Some plant species apparently benefit more than others, and some do not benefit at all. For instance, removing ants from six myrmecophytic *Macaranga* species in Southeast Asia increases herbivore damage by anywhere from 0–10 percent and vine coverage from 5–30 percent across species (Fiala *et al.* 1991). Variation in benefit is equally striking, however, within individual plant species studied at different times and places. Horvitz and Schemske (1984), for example, demonstrated considerable spatial variation in the benefits of ants visiting extrafloral nectaries of *Calathea ovandensis* at sites located less than 500 m apart in Mexican secondary forest. While similar intraspecific variation in benefit has been noted in many other forms of mutualism (Thompson 1988, Bronstein 1994b), it has been most thoroughly documented in ant-plant protective mutualisms (Beattie 1985, Cushman 1991, Cushman & Addicott 1991).

Such variation appears to be a general phenomenon of major significance for understanding how mutualisms function and evolve (Bronstein 1994b). While mutualisms are commonly defined as mutually beneficial interactions, they simultaneously involve major costs as well. For instance, in ant-plant protective mutualisms, plants produce food rewards for ants at measurable metabolic costs to themselves (see following). Spatial or temporal variation in the magnitude of either the costs or

the benefits of the interaction will change the net effect for each partner, which can be thought of as the benefit of the interaction minus its cost. The interaction can therefore range from strong to weak mutualism, and even into commensalism and antagonism. While such variation in the outcome of interactions (often referred to as "conditionality") has been copiously documented (e.g., Thompson 1988, Cushman & Addicott 1991, Bronstein 1994b), the degree to which this conditionality is predictable, and what ecological variables regulate it, are less certain. Here again, the little we know has emerged largely from studies of ant-plant protection mutualisms. I discuss three causes of variation in the advantages of mutualism, using ant-plant protective interactions as examples. I then consider whether these interactions might be particularly prone to variation in benefits.

VARIATION IN PARTNER SPECIES.—Few mutualisms involve one-to-one correspondences between species. The first and perhaps most important source of variation in mutualism is that alternative partner species provide different magnitudes of benefit. Ant species clearly differ greatly in the quality of protection they confer to plants (Koptur 1984; Heads 1986; Oliveira et al. 1987a, b; Jaffe et al. 1989; Rico-Gray & Thien 1989; Davidson et al. 1991). For instance, Horvitz and Schemske (1984) show that eight ant species facultatively associated with Calathea ovandensis differ almost threefold in their protective abilities; seed production is highest when plants are defended by the smallest ant (Wasmannia auropunctata). Some ant species confer no benefit at all, or even inflict a net cost on their host plants; they may avoid encounters with herbivores and/or use up food and space that would otherwise be available for more mutualistic species (Janzen 1975, Davidson & McKey 1993). Conversely, from the perspective of the ants, different plant species probably vary in attractiveness because of differences in the quality or quantity of food rewards they offer. This phenomenon appears to have been minimally investigated to date (but see Keeler 1981, Fiala & Maschwitz 1990, Yu & Davidson 1997), pointing again to the phytocentric focus of most ant-plant protection studies.

Such variation in the quality of benefits conferred by different partners has been recorded in almost every form of mutualism (e.g., Herrera 1987, Buckley & Guillan 1991, Schupp 1993). However, it has perhaps been quantified most effectively for ant-plant protective interactions, because it is unusually straightforward to contrast the performance of alternative partners objectively: herbivores can be added to the plant and the relative effectiveness of different ant species at removing them can be compared (e.g., Oliveira et al. 1987a, b). A critical need is to develop robust frameworks for predicting such interspecific differences in effectiveness. For myrmecophytic systems, Davidson and McKey (1993) summarize the traits that predict the quality of protection conferred by different ant species. Although they consider existing data to be meager, they suggest that ants with rapid colony development, large colony size, and high levels of worker activity should be better defenders. Ant size and aggressiveness are also critical in determining the kind of protection a species can provide to myrmecophytes (Letourneau 1983; Oliveira et al. 1987a, b; Fiala et al. 1989; Jaffe et al. 1989). Bentley (1977b) offers a similar list of traits predicting the effectiveness of different ant species that facultatively visit extrafloral nectaries.

VARIATION IN MUTUALIST ABUNDANCE.—When its mutualists are excluded entirely, an individual generally suffers; as discussed above, this criterion is the one commonly used to decide that a given interaction is mutualistic. The magnitude of benefit an individual organism experiences in nature, however, depends not only on whether any mutualists are present, but on how many of them there are. Variation in abundance of each mutualist species is the second source of variation in mutualism. Remarkably little is yet known for any mutualism regarding how many partners an individual associates with at once (or over its lifetime), what factors predict this number, whether or not an individual can control it, or how it scales with fitness. The simplest prediction is that success increases steadily with the number of mutualists an organism is able to attract, and that traits increasing its attractiveness will therefore be favored. This prediction is not always supported, however (e.g., Klinkhamer & de Jong 1993), suggesting that much more investigation is warranted. Ant abundance at extrafloral nectaries varies with distance from ant nests (Inouye & Taylor 1979), the presence of alternative sugar sources (Sudd & Sudd 1985), and altitude (Koptur 1984); in at least some cases, herbivore damage decreases steadily with this increase in visitation (Inouye & Taylor 1979). In myrmecophytic systems, there has been some attention paid to factors predicting ant colony size, and how colony size in turn predicts how effectively hosts are protected from herbivore attack. In the most detailed study to date, Duarte Rocha and Godoy Bergallo (1992)
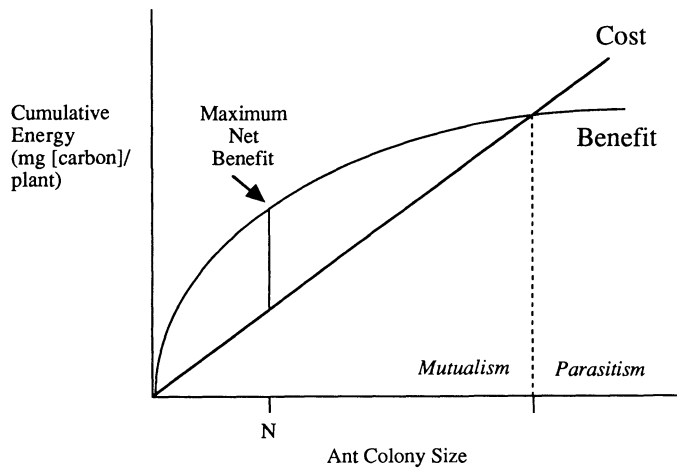
FIGURE 2.   Fonseca's (1993) model of the costs and benefits to myrmecophytic plants of maintaining different colony sizes of protective ants. N is the colony size that produces the greatest net benefit to the plant. Where costs of ant maintenance exceed the benefits ants can provide, the relationship is parasitic rather than mutualistic.

demonstrated that colony size of Brazilian *Azteca muelleri* ants (4–535 individuals) was highly positively correlated with size of their host plants (*Cecropia pachystachya*). When more ants were present, herbivores were located more rapidly and herbivore residence time on leaves declined, leading to a significant reduction in levels of herbivory.

Duarte Rocha and Godoy Bergallo's (1992) data might suggest that the benefit of myrmecophytism increases steadily with the size of the ant colonies that plants host. However, much remains to be investigated. In particular, does protection from herbivore damage in fact result in increased reproductive success? The relationship between defoliation and plant fecundity is rarely straightforward (Crawley 1983, Marquis 1992). Furthermore, Duarte Rocha and Godoy Bergallo (1992) found that the degree of herbivore protection did not increase linearly with ant numbers, but rather appeared to level off at colony sizes >300. Are intermediate and large ant colonies thus equally beneficial for the plant? Fonseca (1993) has argued that the energetic cost of maintaining ants is likely to rise linearly with colony size while benefits of protection will not, resulting in an intermediate optimum colony size from the perspective of the plant (Fig. 2). He provides evidence that domatia volume of two Brazilian myrmecophytes limits ant colony sizes, and suggests that selection may have shaped this trait to increase the plants' net benefit from the interaction.

Fonseca's (1993) model provides valuable predictions about one source of variation in mutual-

ism. Quantitative tests should prove enlightening; it could also be extended to other forms of mutualism. However, attention also should be paid to the selective interests of the other partner, since they may or may not conflict with those of its mutualist. For instance, in the Fonseca (1993) example, it is important to know the optimal colony size from the perspective of the ants and not only the plants. Production of workers declines in efficiency as colony size increases (Michener 1964), and this is a major factor limiting colony size across ants in general (Tschinkel 1993).

It should also be pointed out that we have almost no information about the genetic basis of traits critical in ant-plant interactions (Beattie 1991), or for that matter, in most other mutualisms. Hypotheses for how selection can shape these traits will remain pure speculation until such data are obtained.

VARIATION IN THE NEED FOR MUTUALISTS.—Mutualists are only beneficial when there is a need for the commodity they provide. It is usual, however, for that need to vary in both time and space; this is a third source of variation in mutualism.

Ants obviously can benefit plants only in the presence of plant enemies they can repulse (Bentley 1977b). More specifically, the magnitude of benefit experienced by plants can be expected to scale to some degree with the abundance of plant enemies, their mode of feeding, the degree to which they overlap phenologically with ants, and the cost of the damage they inflict. Rashbrook *et al.* (1991,

1992) consider these factors in attempting to explain why, throughout its range, bracken fern (*Pteridium aquilinum*) appears to benefit minimally, if at all, from the ants that visit its extrafloral nectaries. They conclude that low herbivore densities and consequently low levels of herbivory are at least partially responsible, although low rates of ant visitation may ultimately prove most important. Additions and removals of ants and herbivores allowed Barton (1986) to conclude that reproductive success of *Cassia fasciculata* was significantly increased by ant visitation to extrafloral nectaries only when both ants and herbivores were abundant. Koptur and Lawton (1988) show that ants benefit *Vicia sativa* in England only where the surface-feeding herbivores that they can deter are abundant. In contrast, when internal feeders predominate, ants attack these herbivores' parasitoids and are therefore antagonistic to the plants, rather than mutualistic.

Other aspects of the biotic and abiotic environment are also likely to affect the need for mutualists, although these factors have received minimal study to date. For example, in certain habitats, plants may be able to tolerate more herbivore damage or produce higher levels of defensive chemicals (Marquis 1992). Herbivore and ant identities and abundances will also vary among habitats as functions of their own physiological tolerances (Bentley 1976, Marquis 1992). These factors are likely to interact in a way that results in higher benefits to protective mutualism in certain types of habitats.

THE SCALE AND DISTRIBUTION OF VARIATION IN BENEFITS.—These three sources of variation—in the identity, abundance, and need for partners—evidently combine and interact to generate a complex spatial and temporal mosaic of cost and benefit within mutualisms. The number of variables and scales over which a mutualism must be studied to describe effectively this mosaic is daunting. Researchers have been filling in pieces of this picture for some time, but perhaps the most complete description so far is emerging from Davidson and collaborators' studies of several myrmecophytic *Cecropia* species in Peru (Davidson & Fisher 1991; Davidson *et al.* 1991; Folgarait *et al.* 1994, Folgarait & Davidson 1994, 1995; Yu & Davidson 1997). Spatial variation is particularly striking in this system. Ant communities differ somewhat between riverside and gap habitats, and different members of the ant community vary strikingly in quality as mutualists. Some, but not all, ant species have preferences as to which *Cecropia* species

they colonize, but colonization patterns and frequencies are also affected by a given plant's proximity to foundress sources. Habitat-related variables may also influence levels of herbivory and the success of ant-*Cecropia* interactions once they have become established. Parasite attack on ants is more common in riverside habitats, and host-plant quality—in particular, the amount of reward they produce for ants (see following)—is reduced where light and nutrients are limiting. Yu and Davidson (1997) discuss some of the broader ecological and evolutionary implications of these patterns. They argue that historical coincidences, such as preadapted habitat affiliations of hosts and ants, have been critical in establishing opportunities for diffuse and pairwise coevolution in mutualisms like these.

To what extent is the great variability inherent in ant-plant protective interactions, as well as the evolutionary significance of that variability, representative of mutualisms as a whole? I have offered three predictions for where the outcomes of mutualism are likely to vary most (Bronstein 1994b): (1) outcomes of facultative mutualisms should be more variable than outcomes of species-specific obligate mutualisms, because of inevitable differences in the costs and benefits of associating with alternative partner species and the likely existence of a range of conditions under which partners are either not required or absolutely harmful; (2) mutualisms in which a third species (*e.g.*, an herbivore) is intimately involved are more likely to show conditional outcomes than are other forms of mutualism. In these cases, factors that affect the abundance, behavior, and identity of the third species—not only those affecting abundance, behavior, and identity of mutualists themselves—will potentially shift the mutualism's outcome; and (3) mutualisms in which benefits are functions of the abundance of partners should show greater conditionality than those in which a single individual can satisfy the requirement for reward or service.

As we have seen, ant-plant protective mutualisms would be predicted by all three criteria to have variable outcomes. This observation suggests the more general prediction that protective interactions like these may be the most variable form of mutualism. Comparative studies of less well known protective mutualisms, such as those involving cleaner fish and their hosts (Poulin & Grutter 1996), anemones and anemonefish (Fautin 1991), and grasses and their endophytic fungi (Clay 1990) would be valuable.

VARIATION IN THE COSTS OF MUTUALISM

Studies of mutualism have always focused on the advantages these interactions confer to participants, although, as we have seen, it is only recently that the great ecological variation in these advantages has been recognized and its evolutionary significance considered. However, mutualism can also impose substantial costs on the partners. These include costs of locating, attracting, and rewarding the partners that confer benefits, as well as costs associated with species that exploit the partnership. There is no reason to believe that the costs of mutualism are any less variable in ecological space and time than are the benefits. Hence, to develop a general framework for understanding the conditions that favor the evolution and maintenance of mutualism, it will be crucial to identify these costs, measure them, and study the ecological factors that lead them to vary. Such research has only just begun (*e.g.,* Addicott 1986, Noë & Hammerstein 1994, Fiedler & Saam 1995, Poulin & Vickery 1995, Smith & Smith 1996, Bronstein & Ziv 1997).

One major investment in most mutualisms is the reward produced by one or both species to attract the partners that convey the needed service. Natural history studies of mutualism often focus on identifying such rewards, particularly food substances (nectar in many pollination mutualisms, fruit in seed-dispersal mutualisms, honeydew in ant-homopteran protective mutualisms, etc.). Many other, less system-specific questions, however, can be asked about mutualistic rewards. To what degree has their chemical composition shaped and/or been shaped by the metabolic requirements of partner species? How much do rewards cost to produce, and how do these costs regulate their production dynamics? How variable are the quantity and quality of rewards; does this variability have a genetic basis, and what are its ecological and evolutionary consequences? Can rewards be targeted at the subset of visitors that provide the most effective mutualistic service?

Most of what we know at this point comes from a single type of reward in a single type of mutualism: floral nectar, in plant-pollinator interactions. Hundreds of studies have examined the quantity of nectar that plants produce, how it is dispensed across the day and across flowers within a plant, and how floral traits regulate its access to visitors. Herbert and Irene Baker pioneered the chemical analysis of nectar, showing that its composition is correlated with the major taxon of pollinator that uses it. For example, nectar in bee-pollinated plants is relatively rich in sucrose, while nectar in hummingbird-pollinated flowers is hexose dominated (Baker & Baker 1983a, b). A few attempts have been made to measure the metabolic cost to the plant of producing nectar (Southwick 1984, Pyke 1991); adaptations have been identified that allow plants to reduce these costs (Burquez & Corbet 1991). Interest has recently developed in the causes and consequences of intraspecific variation in nectar volume and chemistry; some of the variation is probably genetic (Hodges 1993, Boose 1997), but much of it results from local variation in water and nutrient availability (Pleasants & Chaplin 1983, Wyatt *et al.* 1992, Boose 1997). Flower visitors are often very sensitive to this variation. They avoid plants offering lesser or poorer rewards (*e.g.,* Mitchell 1993, Ackerman *et al.* 1994, Hodges 1995) and remain so long on those plants offering high rewards that most of the pollen they transfer is self-pollen (Klinkhamer & de Jong 1993). Several graphic models have been proposed that attempt to predict how floral nectar rewards will evolve in light of the costs of nectar production and the risk of pollinators overstaying their welcome (Pyke 1981, Possingham 1988, Zimmerman 1988, Rathcke 1992, Hodges 1995). All predict that an intermediate rate of reward production should be optimal. Empirical evidence in support of this prediction is accumulating (Hodges 1995; but see Boose 1997).

To what degree can the predictions of these models be generalized to the other diverse forms of mutualism? To answer this question, we need equally detailed knowledge on the benefits and costs of reward production in other mutualisms. Much relevant work has been conducted with seed dispersal mutualisms. Howe and Estabrook (1977) predicted that fruit-removal rates and hence plant fitness should peak at intermediate fruit-crop sizes, but this hypothesis has rarely been supported in empirical studies (*e.g.,* Murray 1987, Laska & Stiles 1994). This may partially be explained by a lack of concordance between fruit-removal rates and ultimate rates of recruitment (Herrera *et al.* 1994).

Studies of ant-plant protective mutualisms have perhaps greater comparative potential. Information is rapidly accumulating on the chemistry of both extrafloral nectar and certain types of food bodies, as well as on their adaptive nature, although their genetic bases remain largely unexplored. Koptur (1992) has recently summarized the composition of extrafloral nectar and discussed its relation to the

nutritional needs of ant mutualists. Sugar, a quickly and easily utilized source of energy for ants, makes up the largest proportion of solutes, but amino acids are also present and appear important in determining ant preferences (Baker *et al.* 1978, Lanza & Krauss 1984, Lanza *et al.* 1993). Even when they are present in very low concentrations, amino acids in rewards may be the most important source of nitrogen for some kinds of ants (Davidson & Patrell-Kim 1996). Like floral nectar, extrafloral nectar contains substances that may be feeding deterrents or toxins to nonmutualists (Koptur 1992). The chemistry of floral and extrafloral nectars differs somewhat in relation to the divergent nutritional needs of pollinators and defenders, but to some degree, they may be constrained taxonomically; Koptur (1994) has shown that the two types of nectar are more similar than expected within individual Costa Rican *Inga* species.

The composition of rewards produced by myrmecophytes was first examined by Rickson (1971, 1980; Rickson & Risch 1984) and more recently has been studied in an ecological context by Folgarait and co-workers (Folgarait & Davidson 1994, 1995; Folgarait *et al.* 1994). *Cecropia* trees produce both pearl bodies, which are rich in lipids and amino acids, and glycogen-rich Müllerian bodies. Production of these two food bodies is limited in different ways by resource and light availability: pearl body production increases under conditions of low light and high nutrients, whereas Müllerian body rewards increase with both light and nutrient availability (Folgarait & Davidson 1994, 1995). Folgarait and Davidson (1994, 1995) use information about these contrasting costs to test certain predictions from plant defense theory. They argue that resource availability best predicts the mode of defense that is likely to evolve.

Other less direct lines of evidence are also accumulating about the costs of producing ant rewards. On islands where ants are absent, *Cecropia peltata* rarely produces food bodies (Janzen 1973, Rickson 1977, Putz & Holbrook 1988; but see Wetterer 1997); in Hawaii, where there are no native ants, few plant species have functional extrafloral nectaries (Keeler 1984). More surprisingly, some plants produce rewards only when there is a need for them. Three studies (Stephenson 1982, Koptur 1989, Smith *et al.* 1990) have shown that either the volume or chemistry of extrafloral nectar changes after the plants have suffered herbivore damage, suggesting that ant protection is an "inducible defense" against herbivory (*cf.* Harvell 1990, Haukioja 1991). Risch and Rickson (1981)

and Letourneau (1990, 1991) have demonstrated experimentally that in certain Costa Rican *Piper* species, food-body production is induced by the presence of ants. It is not yet known how plants assess their presence, nor whether the probability of reward induction varies according to the species of ant (and thus its quality as a mutualist). Such discrimination is not entirely unreasonable; in one case, a nonmutualistic beetle has apparently circumvented this mechanism and is able to induce food-body production to the detriment of the plant (Letourneau 1990). Production of new Müllerian bodies in some Neotropical *Cecropia* occurs only after the first set has been removed by ants (Folgarait *et al.* 1994), suggesting that investment is withheld if it is not required.

This information about the costs of ant rewards has yet to be incorporated into models predicting optimal levels of investment in these mutualisms. Fonseca (1993) suggests that these costs should increase linearly with the number of ants fed (Fig. 2). If, as he argues, benefits of ant protection level off at high ant numbers, this would imply that intermediate levels of investment should be favored. Hence, predictions about optimal investment in mutualistic rewards would appear to be parallel for pollination, seed dispersal, and ant-protective interactions. Tests of this prediction in ant-plant systems would be valuable, as would attempts to extend this theory to other forms of mutualism.

DISCUSSION

I have argued that a central contribution of ant-plant protection studies has been the development of approaches to measuring benefits, costs, and net outcomes of mutualism, and the recognition and quantification of variability in all of these phenomena. Other important contributions to our understanding of mutualism, however, have been or are currently being pioneered. Some of these are ecologically oriented; these include, for instance, studies on the nature and significance of "cheating" (Janzen 1975, Letourneau 1990, Jolivet 1991) and documentation of the distribution of mutualism at the community, regional, and continental scales (Schupp & Feener 1991, Rico-Gray 1993, McKey & Davidson 1993, Fonseca & Ganade 1996). Other important directions are more evolutionary in focus, such as the identification of conditions favoring the evolution of specificity (Fiala & Maschwitz 1991, 1992; Fiala *et al.* 1994; Fonseca & Ganade 1996; Yu & Davidson 1997) and the development of phylogenetic approaches to understanding the evolution of

mutualism (McKey 1991, Ward 1991). Some of these are new directions in mutualism research, while others are generating comparative data critical for evaluating general theories about mutualism. All of them simultaneously are contributing to a greater understanding of the many tropical ecosystems in which mutualisms figure prominently.

ACKNOWLEDGMENTS

LITERATURE CITED

ACKERMAN, J. D., J. A. RODRIGUEZ-ROBLES, AND E. J. MELÉNDEZ. 1994. A meager nectar offering by an epiphytic orchid is better than nothing. Biotropica 26: 44–49.
ADDICOTT, J. F. 1986. Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. Oecologia (Berl) 70: 486–494.
ALLWARD, R. D., AND A. JOERN. 1993. Plasticity and overcompensation in grass responses to herbivory. Oecologia (Berl) 95: 358–364.
BAKER, H. G., P. A. OPLER, AND I. BAKER. 1978. A comparison of the amino acid complements of floral and extrafloral nectars. Bot. Gaz. 139: 322–332.
———, AND I. BAKER. 1983a. Floral nectar sugar constituents in relation to pollinator type. *In* C. E. Jones and R. J. Little (Eds.). Handbook of experimental pollination biology, pp. 117–141. Van Nostrand Reinhold, New York, New York.
———, AND ———. 1983b. A brief historical review of the chemistry of floral nectar. *In* B. L. Bentley and T. Elias (Eds.). The biology of nectaries, pp. 126–152. Columbia University Press, New York, New York.
BARTON, A. M. 1986. Spatial variation in the effect of ants on an extrafloral nectary plant. Ecology 67: 495–504.
BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge, England.
———. 1991. Problems outstanding in ant-plant interaction research. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 559–572. Oxford University Press, New York, New York.
BELSKY, A. J. 1986. Does herbivory benefit plants? A review of the evidence. Am. Nat. 127: 870–892.
BELT, T. 1874. The naturalist in Nicaragua. Dent and Sons, London, England.
BENTLEY, B. L. 1976. Plants bearing extrafloral nectaries and the associated ant community: interhabitat differences in the reduction of herbivore damage. Ecology 57: 815–820.
———. 1977a. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). J. Ecol. 65: 27–38.
———. 1977b. Extrafloral nectaries and protection by pugnacious bodyguards. Ann. Rev. Ecol. Syst. 8: 407–428.
BERGELSON, J., AND M. J. CRAWLEY. 1992. Herbivory and *Ipomopsis aggregata*: the disadvantages of being eaten. Am. Nat. 139: 870–882.
BOOSE, D. L. 1997. Sources of variation in floral nectar production rate in *Epilobium canum* (Onagraceae): implications for natural selection. Oecologia (Berl) 110: 493–500.
BRONSTEIN, J. L. 1991. Mutualism studies and the study of mutualism. Bull. Ecol. Soc. Am. 72: 6–8.
———. 1994a. Our current understanding of mutualism. Q. Rev. Biol. 69: 31–51.
———. 1994b. Conditional outcomes in mutualistic interactions. Trends Ecol. Evol. 9: 214–217.
———, AND Y. ZIV. 1997. Costs of two non-mutualistic species in a yucca/yucca moth mutualism. Oecologia (Berl) 112: 379–385.
BUCKLEY, R., AND P. GUILLAN. 1991. More aggressive ant species (Hymenoptera, Formicidae) provide better protection for soft scales and mealybugs (Homoptera: Coccidae, Pseudococcidae). Biotropica 23: 282–286.
BURQUEZ, A., AND S. A. CORBET. 1991. Do flowers reabsorb nectar? Funct. Ecol. 5: 369–379.
CRAWLEY, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. University of California Press, Berkeley, California.
CLAY, K. 1990. Fungal endophytes of grasses. Annu. Rev. Ecol. Syst. 21: 275–298.
CUSHMAN, J. H. 1991. Host-plant mediation of insect mutualisms: variable outcomes in herbivore-ant interactions. Oikos 61: 138–144.
———, AND J. F. ADDICOTT. 1991. Conditional interactions in ant-plant-herbivore mutualisms. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 92–103. Oxford University Press, New York, New York.
———, AND A. J. BEATTIE. 1991. Mutualisms: assessing the benefits to hosts and visitors. Trends Ecol. Evol. 6:193–195.
———, V. K. RASHBROOK, AND A. J. BEATTIE. 1994. Assessing benefits to both participants in a lycaenid-ant association. Ecology 75: 1031–1041.
DAVIDSON, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biol. J. Linn. Soc. 61: 153–181.
———, AND S. R. MORTON. 1981. Competition for dispersal in ant-dispersed plants. Science (Wash. DC) 213: 1259–1261.

————, AND W. W. EPSTEIN. 1989. Epiphytic associations with ants. *In* U. Lüttge (Ed.). Vascular plants as epiphytes, pp. 200–233. Springer Verlag, Berlin, Germany.

————, AND B. L. FISHER. 1991. Symbiosis of ants with *Cecropia* as a function of light regime. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 289–309. Oxford University Press, New York, New York.

————, R. B. FOSTER, R. R. SNELLING, AND P. W. LOZADA. 1991. Variable composition of some tropical ant-plant symbioses. *In* P. W. Price, T. W. Lewinsohn, G. W. Fernandes and W. W. Benson (Eds.). Plant-animal interactions: evolutionary ecology in tropical and temperate regions, pp. 145–162. John Wiley & Sons, Inc., New York, New York.

————, AND D. MCKEY. 1993. The evolutionary ecology of symbiotic ant-plant relationships. J. Hym. Res. 2: 13–83.

————, AND L. PATRELL-KIM. 1996. Tropical arboreal ants: why so abundant? *In* A. C. Gibson (Ed.). Neotropical biodiversity and conservation, pp. 127–140. Mildred E. Matthias Botanical Garden, University of California at Los Angeles, Los Angeles, California.

DUARTE ROCHA, C. F., AND H. GODOY BERGALLO. 1992. Bigger ant colonies reduce herbivory and herbivore residence time on leaves of an ant-plant: *Azteca muelleri* vs. *Coelomera ruficornis* on *Cecropia pachystachya*. Oecologia (Berl) 91:249–252.

FAUTIN, D. 1991. The anemone fish symbiosis: what is known and what is not. Symbiosis 10: 23–46.

FIALA, B., U. MASCHWITZ, T. Y. PONG, AND A. J. HELBIG. 1989. Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. Oecologia (Berl) 79: 463–470.

————, and ————. 1990. Studies on the south east Asian ant-plant association *Crematogaster borneensis/Macaranga*: adaptations of the ant partner. Insectes Soc. 37: 212–231.

————, AND ————. 1991. Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytism. Biol. J. Linn. Soc. 44: 287–305.

————, AND ————. 1992. Food bodies and their significance for obligate ant-association in the tree genus *Macaranga* (Euphorbiaceae). Bot. J. Linn. Soc. 110: 61–75.

————, ————, AND T. Y. PONG. 1991. The association between *Macaranga* trees and ants in South-east Asia. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 263–270. Oxford University Press, New York, New York.

————, H. GRUNSKY, U. MASCHWITZ, AND K. E. LINSEMAIR. 1994. Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant protection. Oecologia (Berl) 97: 186–192.

FIEDLER, K., AND C. SAAM. 1995. A "microbial cost" of butterfly-ant mutualisms (Lycaenidae). J. Lep. Soc. 49: 80–84.

FOLGARAIT, P. J., AND D. W. DAVIDSON. 1994. Antiherbivore defenses of myrmecophytic *Cecropia* under different light regimes. Oikos 71: 305–320.

————, AND ————. 1995. Myrmecophytic *Cecropia*: antiherbivore defenses under different nutrient treatments. Oecologia (Berl) 104: 189–206.

————, H. L. JOHNSON, AND D. W. DAVIDSON. 1994. Responses of *Cecropia* to experimental removal of Müllerian bodies. Funct. Ecol. 8: 22–28.

FONSECA, C. R. 1993. Nesting space limits colony size of the plant-ant *Pseudomyrmex concolor*. Oikos 67: 473–482.

————, AND G. GANADE. 1996. Asymmetries, compartments and null interactions in an Amazonian ant-plant community. J. Anim. Ecol. 65: 339–347.

GÓMEZ, J. M., AND R. ZAMORA. 1992. Pollination by ants: consequences of the quantitative effects on a mutualistic system. Oecologia (Berl) 91: 410–418.

HANZAWA, F. M., A. J. BEATTIE, AND D. C. CULVER. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. Am. Nat. 131: 1–13.

HARTNETT, D. C., R. J. SAMENUS, L. E. FISCHER, AND B. A. D. HETRICK. 1994. Plant demographic responses to mycorrhizal symbiosis in tallgrass prairie. Oecologia (Berl) 99: 21–26.

HARVELL, C. D. 1990. The ecology and evolution of inducible defenses. Q. Rev. Biol. 65: 323–340.

HAUKIOJA, E. 1991. Induction of defenses in trees. Annu. Rev. Ent. 36: 25–42.

HEADS, P. E. 1986. Bracken, ants and extrafloral nectaries. IV. Do wood ants (*Formica lugubris*) protect the plant against insect herbivores? J. Anim. Ecol. 55: 795–809.

HERRERA, C. M. 1987. Components of pollinator "quality": comparative analysis of a diverse insect assemblage. Oikos 50: 79–90.

————, P. JORDANO, L. LOPEZ-SORIA, AND J. A. AMAT. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecol. Monogr. 64: 315–344.

HODGES, S. A. 1993. Consistent interplant variation in nectar characteristics of *Mirabilis multiflora*. Ecology 74: 542–548.

————. 1995. The influence of nectar production on hawkmoth behavior, self pollination, and seed production in *Mirabilis multiflora* (Nyctaginaceae). Am. J. Bot. 82: 197–204.

HORVITZ, C. C., AND D. W. SCHEMSKE. 1984. Effects of ants and an ant-tended herbivore on seed production of a Neotropical herb. Ecology 65: 1369–1378.

HOWE, H. F., AND G. F. ESTABROOK. 1977. On intraspecific competition for avian dispersers in tropical trees. Am. Nat. 111: 817–832.

HUGHES, L., AND M. WESTOBY. 1992. Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. Ecology 73: 1285–1299.

INOUYE, D. W., AND O. R. TAYLOR, JR. 1979. A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. Ecology 60: 1–7.

JAFFE, K., C. PAVIS, G. VANSUYT, AND A. KERMARREC. 1989. Ants visit extrafloral nectaries of the orchid *Spathoglotis plicata* Blume. Biotropica 21: 278–279.

JANZEN, D. H. 1966. Co-evolution of mutualism between ants and acacias in Central America. Evolution 20: 249–275.
————. 1967a. Fire, vegetation structure and the ant-*Acacia* interaction in Central America. Ecology 48: 26–35.
————. 1967b. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Univ. Kansas Sci. Bull. 47: 315–558.
————. 1973. Dissolution of mutualism between *Cecropia* and its *Azteca* ant. Biotropica 5: 15–28.
————. 1975. *Pseudomyrmex nigropilosa*: a parasite of a mutualism. Science (Wash. DC) 188: 936–937.
JOLIVET, P. 1991. Ants, plants, and beetles: a triangular relationship. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 397–406. Oxford University Press, New York, New York.
KEELER, K. H. 1981. Infidelity by acacia-ants. Biotropica 13: 79–80.
————. 1984. Extrafloral nectaries on plants in communities without ants: Hawaii. Oikos 44: 407–414.
KLINKHAMER, P. G. L., AND T. J. DE JONG. 1993. Attractiveness to pollinators: a plant's dilemma. Oikos 66: 180–184.
KOPTUR, S. 1984. Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. Ecology 65: 1787–1793.
————. 1989. Is extrafloral nectar production an inducible defense? *In* J. H. Bick and Y. B. Linhart (Eds.). The evolutionary ecology of plants, pp. 323–339. Westview Press, Boulder, Colorado.
————. 1992. Extrafloral nectary-mediated interactions between insects and plants. *In* E. Bernays (Ed.). Insect-plant interactions, Vol. IV, pp. 81–129. CRC Press, Boca Raton, Florida.
————. 1994. Floral and extrafloral nectars of Costa Rican *Inga* trees: a comparison of their constituents and composition. Biotropica 26: 276–284.
————, AND J. H. LAWTON. 1988. Interactions among vetches bearing extrafloral nectaries, their biotic protective agents, and herbivores. Ecology 69: 278–283.
LANZA, J., AND B. R. KRAUSS. 1984. Detection of amino acids in artificial nectars by two tropical ants, *Leptothorax* and *Monomorium*. Oecologia (Berl) 63: 423–425.
————, E. VARGO, S. PULIM, AND Y. Z. CHANG. 1993. Responses of the fire ants *Solenopsis invicta* and *S. germinata* (Hymenoptera: Formicidae) for amino acid and sugar components of extrafloral nectaries. Ecol. Entomol. 22: 411–417.
LASKA, M. S., AND E. W. STILES. 1994. Effects of fruit crop size on intensity of fruit removal in *Viburnum prunifolium* (Caprifoliaceae). Oikos 69: 199–202.
LETOURNEAU, D. K. 1983. Passive aggression: an alternative hypothesis for the *Piper-Pheidole* association. Oecologia (Berl) 60: 122–126.
————. 1990. Code of ant-plant mutualism broken by parasite. Science (Wash. DC) 248: 215–217.
————. 1991. Parasitism of ant-plant mutualisms and the novel case of *Piper*. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 390–406. Oxford University Press, New York, New York.
LEVEY, D. J., AND M. M. BYRNE. 1993. Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74: 1802–1812.
MAHDI, T., AND J. B. WHITTAKER. 1993. Do birch trees (*Betula pendula*) grow better if foraged by wood ants? J. Anim. Ecol. 62: 101–116.
MARQUIS, R. J. 1992. Selective impact of herbivores. *In* R. S. Fritz and E. L. Simms (Eds.). Plant resistance to herbivores and pathogens: ecology, evolution, and genetics, pp. 301–325. University of Chicago Press, Chicago, Illinois.
MCKEY, D. 1988. Promising new directions in the study of ant-plant mutualisms. *In* W. Greuter and B. Zimmer (Eds.). Proceedings of the XIV International Botanical Congress, pp. 335–355. Koeltz, Königstein/Taunus, Germany.
————. 1991. Phylogenetic analysis of the evolution of a mutualism: *Leonardoxa* (Leguminosae: Caesalpiniodeae) and its associated ants. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 310–334. Oxford University Press, New York, New York.
————, AND D. W. DAVIDSON. 1993. Ant-plant symbioses in Africa and the Neotropics: history, biogeography and diversity. *In* P. Goldblatt (Ed.). Biological relationships between Africa and South America, pp. 568–606. Yale University Press, New Haven, Connecticut.
MICHENER, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. Insectes Soc. 11: 317–341.
MITCHELL, R. J. 1993. Adaptive significance of *Ipomopsis aggregata* nectar production: observation and experiment in the field. Evolution 47: 25–35.
MURRAY, K. G. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. Am. Nat. 129: 18–31.
NEWSHAM, K. K., A. H. FITTER, AND A. R. WATKINSON. 1994. Root pathogenic and arbuscular mycorrhizal fungi determine fecundity of asymptomatic plants in the field. J. Ecol. 82: 805–814.
NOE, R., AND P. HAMMERSTEIN. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav. Ecol. Sociobiol. 35: 1–11.
O'DOWD, D. J. 1979. Foliar nectar production and ant activity on a neotropical tree, *Ochroma pyramidale*. Oecologia (Berl) 43: 233–248.
OLIVEIRA, P. S., A. T. OLIVEIRA-FILHO, AND R. CINTRA. 1987a. Ant-foraging on ant-inhabited *Triplaris* (Polygonaceae) in western Brazil: a field experiment using live termite-baits. J. Trop. Ecol. 3: 193–200.
————, A. F. DA SILVA, AND A. B. MARTINS. 1987b. Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential antiherbivore agents. Oecologia (Berl) 74: 228–230.
OWEN, D. F. 1980. How plants may benefit from the animals that eat them. Oikos 35: 230–235.
PAIGE, K. N., AND T. G. WHITHAM. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. Am. Nat. 129: 407–416.

PEAKALL, R., AND A. J. BEATTIE. 1991. The genetic consequences of worker ant pollination in a self-compatible, clonal orchid. Evolution 45: 1837–1848.

PLEASANTS, J. M., AND S. J. CHAPLIN. 1983. Nectar production rate of *Asclepias quadrifolia*: causes and consequences of individual variation. Oecologia (Berl) 59: 232–238.

POSSINGHAM, H. P. 1988. A model of resource renewal and depletion: applications to the distribution and abundance of nectar in flowers. Theor. Pop. Biol. 33: 138–160.

POULIN, R., AND W. L. VICKERY. 1995. Cleaning symbiosis as an evolutionary game: to cheat or not to cheat? J. Theor. Biol. 175: 63–70.

————, AND A. S. GRUTTER. 1996. Cleaning symbioses: proximate and adaptive explanations. Bioscience 46: 512–517.

PUTZ, F. E., AND N. M. HOLBROOK. 1988. Further observations on the dissolution of mutualism between *Cecropia* and its ants: the Malaysian case. Oikos 53: 121–125.

PYKE, G. H. 1981. Optimal nectar production in a hummingbird pollinated plant. Theor. Pop. Biol. 20: 326–343.

————. 1991. What does it cost a plant to produce floral nectar? Nature 350: 58–59.

RASHBROOK, V. K., S. G. COMPTON, AND J. H. LAWTON. 1991. Bracken and ants: why is there no mutualism? In C. R. Huxley and D. F. Cutler (Eds.) Ant-plant interactions, pp. 231–237. Oxford University Press, New York, New York.

————, ————, AND ————. 1992. Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. Ecology 73: 2167–2174.

RATHCKE, B. J. 1992. Nectar distributions, pollinator behavior, and reproductive success. In M. D. Hunter, T. Ohgashi and P. W. Price (Eds.). Effects of resource distribution on animal-plant interactions, pp. 113–138. Academic Press, New York, New York.

RICKSON, F. R. 1971. Glycogen plastids in Müllerian body cells of *Cecropia peltata*—a higher green plant. Science 173: 344–347.

————. 1977. Progressive loss of ant-related traits of *Cecropia peltata* on selected Caribbean islands. Am. J. Bot. 64: 585–592.

————. 1980. Developmental anatomy and ultrastructure of the ant-food bodies (Beccarian bodies) of *Macaranga triloba* and *M. hypoleuca* (Euphorbiaceae). Am. J. Bot. 67: 285–292.

————, AND S. J. RISCH. 1984. Anatomical and ultrastructural aspects of the ant-food cell of *Piper coenocladum* C. DC. (Piperaceae). Am. J. Bot. 71: 1268–1274.

RICO-GRAY, V. 1993. Use of plant-derived food resources by ants in the dry tropical lowlands of coastal Veracruz, Mexico. Biotropica 25: 301–315.

————, AND L. B. THIEN. 1989. Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). Oecologia (Berl) 81: 487–489.

RISCH, S. J., AND F. R. RICKSON. 1981. Mutualism in which ants must be present before plants produce food bodies. Nature 291: 149–150.

SCHUPP, E. W. 1986. *Azteca* protection of *Cecropia*: ant occupation benefits juvenile trees. Oecologia (Berl) 70: 379–385.

————. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15–29.

————, AND D. H. FEENER, JR. 1991. Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. In C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 175–197. Oxford University Press, New York, New York.

SMITH, F. A., AND S. E. SMITH. 1996. Mutualism and parasitism: diversity in function and structure in the "arbuscular" (VA) mycorrhizal symbiosis. Adv. Bot. Res. 22: 1–43.

SMITH, L. L., J. LANZA, AND G. C. SMITH. 1990. Amino acid concentrations in the extrafloral nectar of *Impatiens sultani* increase after simulated herbivory. Ecology 71: 107–115.

SOUTHWICK, E. E. 1984. Photosynthate allocation to floral nectar: a neglected energy investment. Ecology 65: 1775–1779.

STEPHENSON, A. G. 1982. The role of extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. Ecology 63: 663–669.

SUDD, J. H., AND M. E. SUDD. 1985. Seasonal changes in the response of wood-ants (*Formica lugubris*) to sucrose baits. Ecol. Entomol. 10: 89–97.

THOMPSON, J. N. 1988. Variation in interspecific interactions. Annu. Rev. Ecol. Syst. 19: 65–87.

TSCHINKEL, W. R. 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. Ecol. Monogr. 63: 425–457.

VASCONCELOS, H. L. 1991. Mutualism between *Maieta guianensis* Aubl., a myrmecophytic melastome, and one of its ant inhabitants: ant protection against insect herbivores. Oecologia (Berl) 87: 295–298.

WARD, P. S. 1991. Phylogenetic analysis of ant-plant associations involving pseudomyrmecine ants. In C. R. Huxley and D. F. Cutler (Eds.). Ant-plant interactions, pp. 335–352. Oxford University Press, New York, New York.

WETTERER, J. K. 1997. Ants on *Cecropia* in Hawaii. Biotropica 29: 128–132.

WYATT, R., S. B. BROYLES, AND G. S. DERDA. 1992. Environmental influences on nectar production in milkweeds (*Asclepias syriaca* and *A. exaltata*). Am. J. Bot. 79: 636–642.

YU, D. W., AND D. W. DAVIDSON. 1997. Experimental studies of species-specificity in *Cecropia*-ant relationships. Ecol. Mongr. 67: 273–294.

ZIMMERMAN, M. 1988. Nectar production, flowering phenology, and strategies for pollination. In J. Lovett Doust and L. Lovett Doust (Eds.). Plant reproductive ecology, pp. 157–178. Oxford University Press, New York, New York.